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A new specimen of trematosaurian temnospondyl from the Lower Triassic of NW Madagascar, with remarks on palatal anatomy and taxonomic affinities

Abstract - A new partial skull (preserved as a natural mould) of a trematosaurid temnospondyl from the Lower Triassic of the Ankitokazo Basin, Diégo Suarez Province, NW Madagascar, is described. It provides new information on the palatal anatomy, poorly known in the Malagasy trematosaurids, the more important concerning the morphology of the cultriform process, which is squared in cross section and comparatively wide. The new specimen represents a taxon well distinct from both Malagasy lonchorhynchine trematosaurid *Wantzosaurus elongatus* and other trematosaurid genera known out of Madagascar. The taxonomic and phylogenetic affinities found between the new skull and all the Malagasy non-lonchorhynchine specimens so far described suggest that the material may belong to a single species, closely related to the German species *Trematolestes hagdorni*, and more similar to *Tertrema acuta* than to *Trematosaurus brauni*. The new skull is therefore tentatively referred to cf. *Tertremoides madagascariensis*, the only non-lonchorhynchine trematosaurid species from Madagascar that we regard as valid, following the systematic review by Schoch & Milner (2000).

Key words: Trematosauridae, Lower Triassic, NW Madagascar, palatal anatomy, cf. *Tertremoides madagascariensis*.

Riassunto - Un nuovo esemplare di temnospondilo trematosauriano del Triassico inferiore del Madagascar nord-occidentale, con commenti sull'anatomia del palato e sulle affinità tassonomiche.

Viene qui descritto un nuovo cranio parziale, conservato come modello, di un temnospondilo trematosauride del Triassico inferiore del bacino di Ankitokazo, Provincia di Diégo Suarez, Madagascar nord-occidentale. L'esemplare fornisce nuovi dati sull'anatomia del palato, regione fino ad oggi poco conosciuta nei trematosauridi malgasci. L'aspetto più importante riguarda la morfologia del processo cultriforme del parasfenoide, che è squadrato in sezione trasversale e relativamente ampio. Il nuovo esemplare rappresenta un taxon ben distinto sia dalla specie malgascia dal muso allungato *Wantzosaurus elongatus*, sia dagli altri trematosauridi non malgasci sinora noti. Le affinità tassonomiche e filogenetiche riscontrate tra il nuovo cranio e tutti gli esemplari di trematosauridi malgasci dal muso non allungato ad oggi descritti suggeriscono inoltre che tutto il materiale potrebbe appartenere ad un'unica specie, strettamente imparentata alla forma tedesca *Trematolestes hagdorni* e più affine a *Tertrema acuta* che a *Trematosaurus brauni*. Il nuovo esemplare è perciò provvisoriamente riferito a cf. *Tertremoides madagascariensis*, unica specie di trematosauride Malgascio dal muso non allungato che consideriamo valida seguendo la revisione sistematica di Schoch & Milner (2000).

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Parole chiave: Trematosauridae, Triassico inferiore, NO Madagascar, anatomia del palato, cf. *Tertremoides madagascariensis*.

Introduction

Malagasy Trematosauroida (*sensu* Yates & Warren, 2000) are known since Lehman (1961, 1966, 1979), who listed the presence of seven different genera in the Lower Triassic of NW of the island. With the exception of *Lyrosaurus*, which is in all likelihood a junior synonym of the rhytidosteid *Mahavisaurus* (Cosgriff & Zawiskie, 1979; Maganuco *et al.*, in prep.), the other six genera are based on genuine trematosaurid material. As reported by several authors (e.g., Steyer, 2002), however, Lehman overestimated the number of the Malagasy trematosaurid taxa, which can be reconducted to two morphotypes only: a gaharial-like morphotype with very elongate rostrum, especially in the prenarial portion; a second one, with rostrum comparatively short in respect to those of the gaharial-like forms.

The long-snouted, gaharial-like material was recently redescribed by Steyer (2002) and belongs to a single species of lonchorhynchine trematosaurid, *Wanzosaurus elongatus* Lehman, 1961. Aside from the holotypic, adult skull, Steyer (2002) described a partial skeleton of a juvenile individual, adding considerable information to the anatomy and ontogeny of the species, as well as to the phylogeny of the trematosaurids. Actually, *Wanzosaurus elongatus* represents the only undisputed, well-characterized Malagasy trematosaurid. According to Schoch & Milner (2000), it includes also two junior synonyms, each one erected by Lehman (1966) on the basis of a single, fragmentary skull roof: *Ifasaurus elongatus* (Lehman, 1966: pl. V B) and *Aphaneramma* sp. (Lehman, 1966: pl. VII D).

The other three Malagasy taxa originally listed and described as Malagasy trematosaurids are the species *Trematosaurus madagascariensis* Lehman, 1966 and *Tertremoides ambilobensis* Lehman, 1979, and material referred by Lehman (1979) to the genus *Tertrema*.

Material referred to *Trematosaurus madagascariensis* includes several specimens: a skull in dorsal view lacking the tip of the snout and part of the right side (Lehman 1966, pl. IV B); skull and mandible at closed jaws lacking part of the posterior half of the postorbital region (holotype - Lehman 1966, pl. V B; pl. VI A, B); a complete skull preserved in dorsal and occipital views (Lehman 1979, pl. II A, B); and a partial skull roof and mandible preserving also some dorsal scutes (Janvier, 1992: pl. I, pl. II-1).

Malagasy material referred to *Tertrema* consists of a single rostral portion of a snout, visible in dorsal and palatal view (Lehman, 1979: figs. 1, 2; pl. I A, B).

Tertremoides ambilobensis is represented by a single but almost complete skull roof, with the dorsal half of the mandible visible in lateral view (Lehman, 1979: fig. 4, pl. III A, B).

The synonymy of Lehman's species *Trematosaurus madagascariensis* and *Tertremoides ambilobensis* was proposed by Schoch & Milner (2000: 115), on the basis of the "similar morphology of the postorbital skull table and the course and expression of the lateral line sulci". Those authors referred all the material to the genus *Tertremoides*, under the combination *Tertremoides madagascariensis*, because of the many differences respect to the genus *Trematosaurus*. Schoch & Milner (2000) listed under the genus *Tertrema*, without any detailed comments, the snout-tip previously referred to *Tertrema* by Lehman (1979).

About the presence of *Tertrema* in Madagascar, Steyer (2002) reported that the material, subsequently to Lehman (1979), was considered as an indeterminate trematosaurid by several authors (for a summary see Steyer, 2002). Steyer (2002) also suggested that *T. madagascariensis* might be a juvenile individual of *Trematosaurus brauni* - the differences between the two species possibly being linked to the immaturity of the Malagasy specimens - but he retained the former as a distinct species, pending a systematic review of the material. Steyer (2002) considered *Tertremoides ambilobensis* as an invalid taxon, diagnosed on characters (e.g., non-confluent infra and supra-occipital sensory-line grooves, comparatively large orbits, ornamentation lacking tubercles, concave occipital margin of the skull) that vary in relation to the ontogenetic stage (see also Steyer, 2000), and therefore possibly representing a late juvenile of *Trematosaurus madagascariensis* or an early juvenile of *Trematosaurus brauni* (if *T. madagascariensis* is really a juvenile of *Trematosaurus brauni*).

More recently, Schoch (2006) concurred with Schoch & Milner (2000) in recognizing *Tertremoides madagascariensis* as the only valid species. The results of his phylogenetic analysis of trematosaurid, which takes into account also the ontogenetic problem in coding character states, show that *Tertremoides madagascariensis* is more derived and well distinct from *Trematosaurus brauni*, and shows close affinities with *Trematolestes hagdorni* from the Middle Triassic of Germany (younger in Age).

Here we describe a new partial skull representing the first Malagasy non-*Wantzosaurus* trematosaurid specimen that preserves, exposed in palatal (ventral) view, the portion of the palate comprised between the posterior margin of the anterior palatal vacuities and the anterior margin of the subtemporal fenestra. This allows us to deepen the knowledge of the anatomy of the Malagasy trematosaurids and to further investigate their questioned taxonomic and phylogenetic affinities.

Material and methods

The specimen is catalogued in the Vertebrate Palaeontological Collection of the Museo di Storia Naturale di Milano (acronym MSNM V) under the number MSNM V2993. The specimen, preserved as a natural mould in a non-calcareous, siliceous, sub-triangular nodule split open in two halves (Fig. 1), has been casted in negative with elastomer for the study. The morphological characters described below refer to this cast, which is a faithful representation of the original skeletal anatomy. Due to this kind of preservation, however, no information about labyrinthine infolding as well as pulp cavities of the preserved teeth is available. The nodule was sampled on surface by local collectors in the 1990's. It is reported from the right bank of the Ifasy River, few kilometres NE to the Anaborano village, Ankitokazo Basin (Besairie, 1972), Ambilobe region, Diégo Suarez Province, Northwestern Madagascar (Fig. 2) (see Maganuco *et al.*, in press, for more details on the locality and faunal assemblage). According to the frequent associated occurrence of the conchostracan *Eustheria (Magniestheria) truempyi* - also known in the Bernburg Formation, lowermost Olenekian of Germany - in the nodules coming from the Ankitokazo Basin, both specimen studied and other Malagasy trematosaurid material listed above can be generally referred to the Olenekian (Yanbin *et al.*, 2002), 249.7 - 245 MA following the ICS stratigraphy (Gradstein *et al.*, 2004), and not to the Induan as previously reported (e.g., Schoch & Milner, 2000), pending other stratigraphic markers and lacking more complete stratigraphic and geological data.

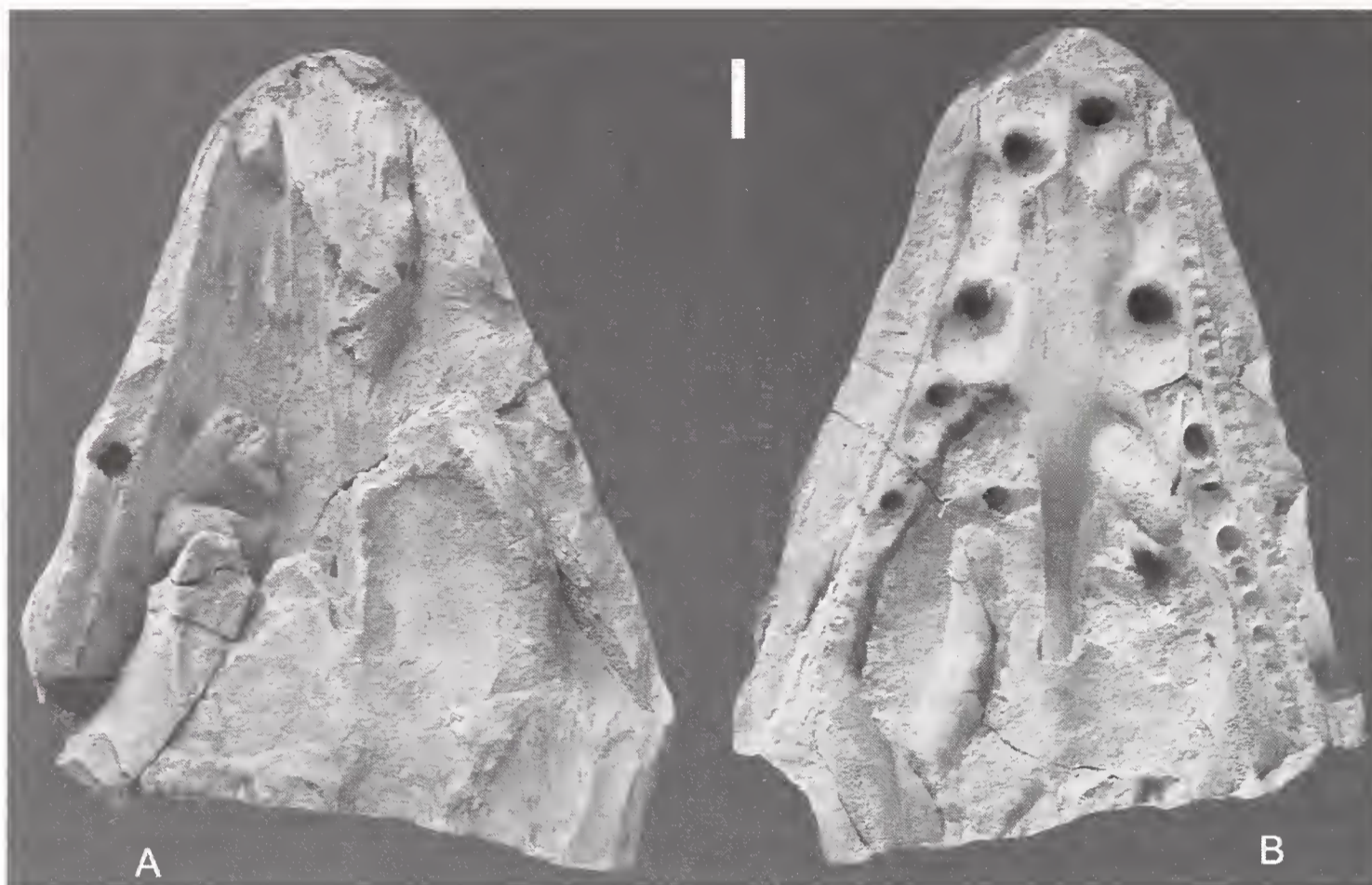


Fig. 1 - Photographs of the specimen MSNM V2993. The nodule, split open, shows the natural mould of the ventral surface of both skull roof (A) and palate (B) of a trematosaurid partial skull. Scale bar equals 20 mm. (Photographs by SM). / Foto dell'esemplare MSNM V2993. Il nodulo, aperto a metà, contiene l'impronta naturale della superficie ventrale del tetto cranico (A) e del palato (B) di un cranio parziale di trematosauride. La scala metrica equivale a 20 mm. (Foto di SM).

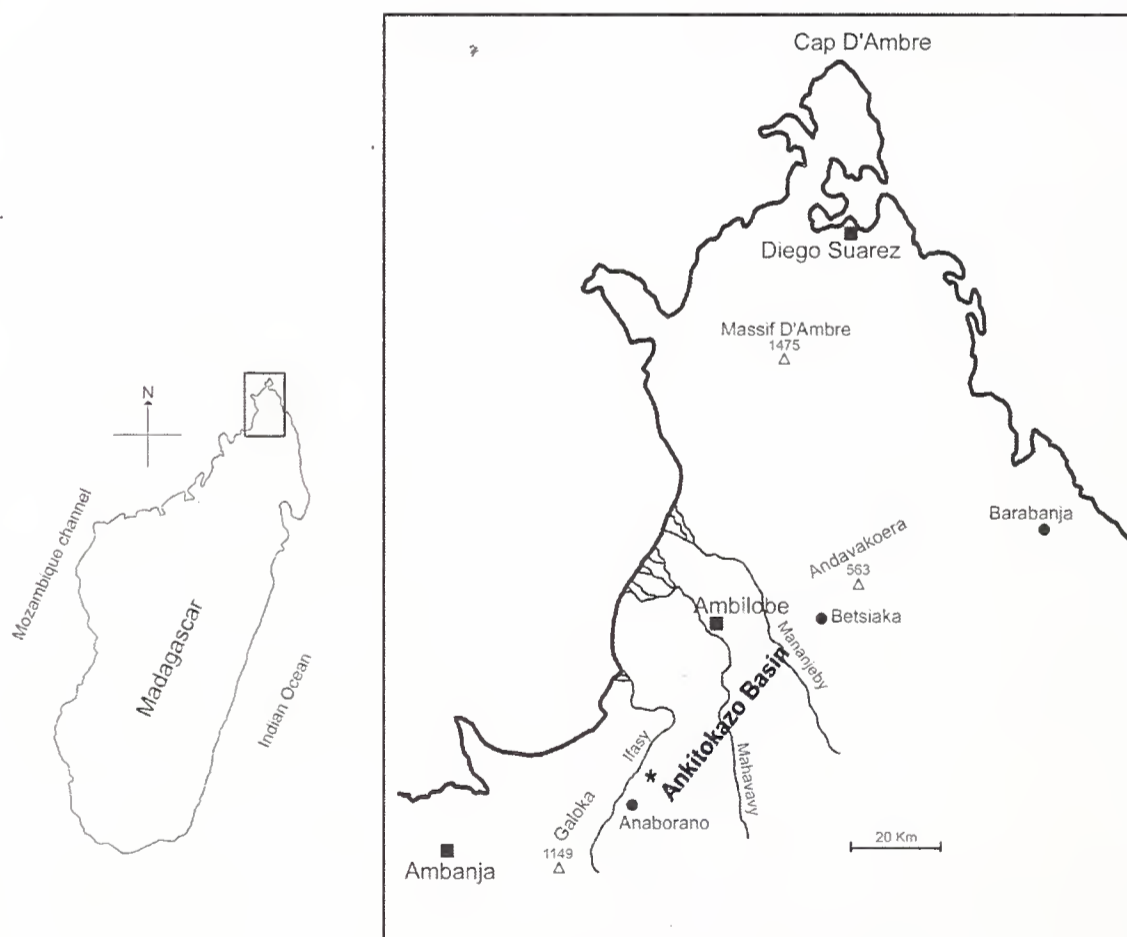


Fig. 2 - Geographic map of Madagascar and close-up of the NW of the island near the village of Anaborano. The main localities and landscape elements cited in the text are shown in the map. The asterisk marks approximately the area from where the specimen MSNM V2993 was collected. (Drawings by F. Nodo).
 Fig. 2 - Carta geografica del Madagascar e particolare del nord-ovest dell'isola nei pressi del villaggio di Anaborano, dove sono evidenziati le principali località e i toponimi citati nel testo. L'asterisco indica approssimativamente la zona da cui proviene l'esemplare MSNM V2993. (Disegno di F. Nodo).

Systematic Palaeontology

Temnospondyli Zittel 1887-1890 (*sensu* Milner, 1990)

Stereospondyli Zittel 1887-1890 (emend. Fraas, 1889)

Trematosauridae Watson, 1919

cf. *Tertremoides madagascariensis* (Lehman, 1966) Schoch & Milner, 2000
Figs. 1, 3, 4.

Trematosaurus madagascariensis Lehman 1966, pl. IV B, V B; VI A, B;
Lehman 1979, pl. II A; Janvier, 1992: pl. I, pl. II-1.

Tertremoides ambilobensis Lehman, 1979, fig. 4, pl. III A, B.

Taxonomic remarks - We concur with Schoch & Milner (2000) that comparisons of the cranial material from the Early Triassic of NW Madagascar previously referred to the genera *Tertremoides* and *Trematosaurus* (see introduction) do not reveal significant differences within those taxa; on the basis of the present knowledge, there is no evidence for the occurrence of more than one monospecific genus of trematosaurids other than *Wantzosaurus elongatus*. Following Schoch & Milner (2000; see introduction), *Tertremoides madagascariensis* is the only species we regard as valid and to which the above listed material must be referred, pending new more complete material and a redescription of Lehman's specimens. Therefore, we cautiously refer to this taxon the new specimen MSNM V2993 as well as the snout tentatively referred by Lehman (1979: figs. 1, 2; pl. I A, B) to *Tertrema* (see discussion).

Description and comparisons

The specimen MSNM V2993 represents an incomplete, sub-triangular, and narrow skull, 177 mm long and 120 mm wide, lacking the tip of the snout and most of the postorbital region. It is one of the largest trematosaur specimens found up to today in Madagascar, comparable in size to the large specimen MNHN MAE 3045 figured by Janvier (1992).

Skull roof (Fig. 3) - MSNM V2993 exposes the ventral surface of the skull roof. For this reason, no details of the skull roof external ornamentation can be seen, and only possible traces of the lateral-line system are visible. The bone surface is worn and damaged, rendering impossible to clearly identify the cranial sutures with the exception of few short traits. Therefore, most of the description of the skull roof is focussed on general outline, cranial openings, and preservation.

The antorbital portion of the skull is mostly incomplete on the left side. The left nasal, as well as bones and structures anterior to it, are almost entirely missing, giving insight to the dorsal aspect of the palate below. A large, unidentified, worn bone is juxtaposed on the skull roof bones just anterior to the left orbit, obscuring contacts between jugal, lacrimal, and maxilla. Anterior to this unidentified bone, a sub-triangular fragment of the left maxilla, 31 mm long, is exposed, whereas medially part of the prefrontal-frontal complex can be seen. The missing portion of the snout medial to the right maxilla renders it possible to observe the choana in dorsal view. An incised groove preserved in the same position on both sides of the skull roof can be tentatively interpreted as part of the infraorbital sulcus of the lateral-line system. It is almost straight, 1 mm deep, and 2 mm wide, and it is preserved for no more than 30 mm. Two portions of another possible sulcus, interpreted as the supraorbital one, are preserved on the right side of the skull: the anterior portion is located medial to the infraorbital sulcus, and it is straight, 31 mm long, 2 mm wide, and 1 mm deep; the posterior portion parallels the posterior half of the medial margin of the orbit, and it is about 20 mm long, 2 mm wide, and very shallow.

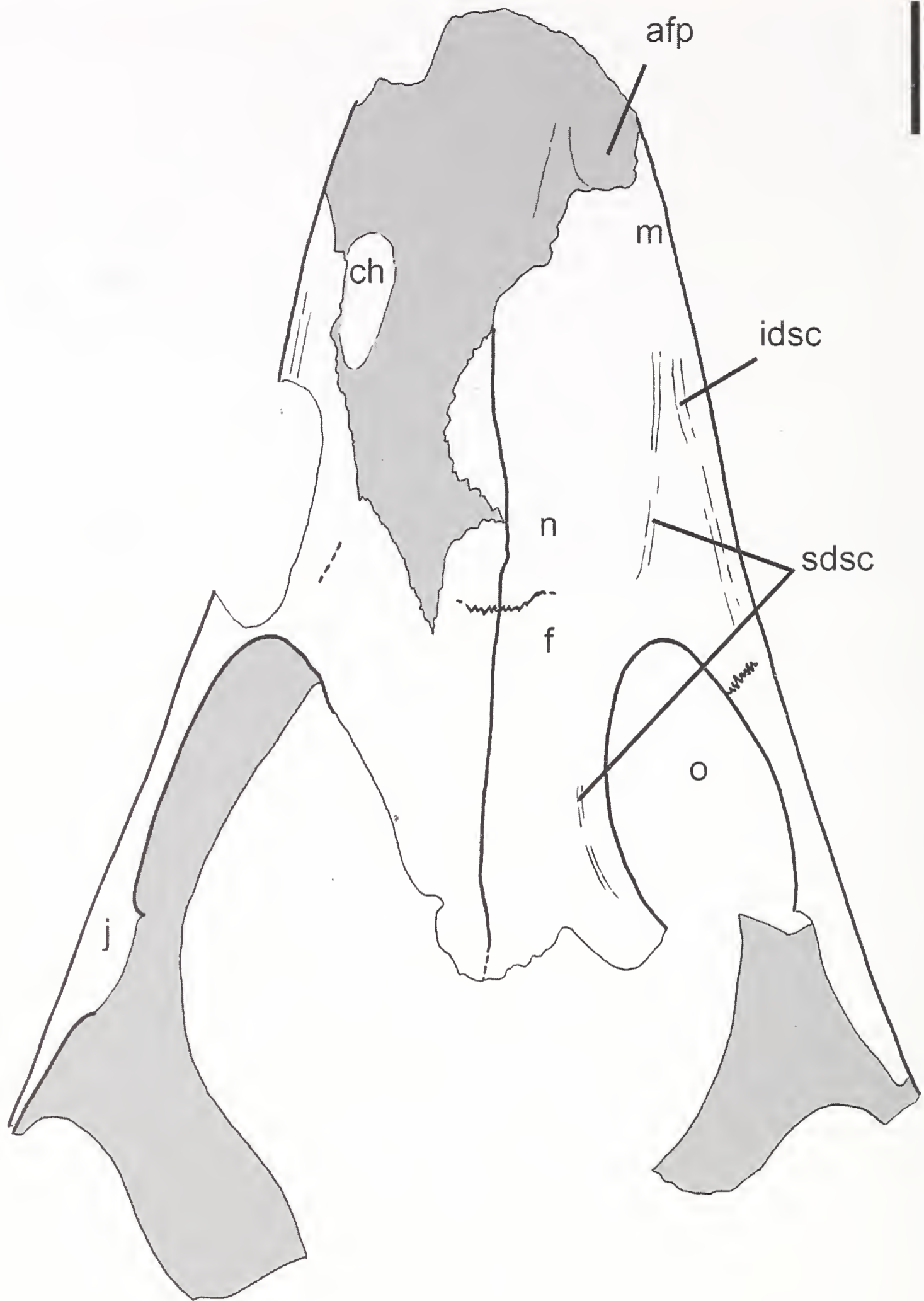


Fig. 3 - Interpretative line-drawing of the specimen MSNM V2993 in dorsal view. Anatomical abbreviations: afp) air-flow passage; ch) choana; f) frontal; idsc) infraorbital dermosensory canal; j) jugal; m) maxilla; n) nasal; o) orbit; sdsc) supraorbital dermosensory canal. Scale bar equals 20 mm. (Drawing by SM).

Fig. 3 - Disegno interpretativo dell'esemplare MSNM V2993 in norma dorsale. Abbreviazioni anatomiche: afp) condotti per il passaggio dell'aria; ch) coana; f) frontale; idsc) canale dermosensoriale infraorbitale; j) giugale; m) mascellare; n) nasale; o) orbita; sdsc) canale dermosensoriale sopraorbitale. La scala metrica equivale a 20 mm. (Disegno di SM).

The snout of MSNM V2993 is more complete on the right side. The right nasal is the most distinguishable element, although its sutures with the neighbouring bones can be only hypothesized. It measures 51 mm in length, and we estimate that it is preserved up to few millimetres posterior to the posterior margin of the naris. Anterior to the anterior broken margin of the nasal, the air-flow passage that united the naris to the choana can be seen on the dorsal surface of the palate. The inferred position of the naris, few millimetres anterior to the broken margin of the nasal, is supported by the condition seen in other similar trematosaurids such as *Tertrema acuta* (Wiman, 1917), *Trematosaurus brauni* (Schoch & Milner, 2000), the Malagasy snout referred to *Tertrema* by Lehman (1979), and *Trematolestes hagdorni* (Schoch, 2006): they show close proximity or superimposition of the posterior margin of the naris respect to the anterior portion of the vomer and its large vomerine tusks.

A roughly transverse, 11 mm long, denticulated portion of the nasofrontal suture is visible, crossing the midline of the skull just anterior to the level of the anterior margin of the orbits, and indicating that in MSNM V2993 the frontals are not as anteriorly extended as they are in *Trematosaurus brauni* (Schoch & Milner, 2000: fig. 77), *Trematosaurus madagascariensis* (e.g., Lehman, 1979: fig. 3), and *Trematolestes hagdorni* (Schoch, 2006: fig. 7), or as they are reconstructed in *Tertremoides ambilobensis* (Lehman, 1979: fig. 4). The posterior extension of both frontals and postfrontals cannot be evaluated, pending their posterior portions. Structures usually visible on the ventral surface of the skull roof, such as the supraorbital laminae, are not apparent on the preserved portion of the frontals. Similarly, the contacts between prefrontal, frontal, and postfrontal cannot be detected on both sides.

Most of the jugals are preserved, with a reconstructed length of about 72 mm: the right one shows parts of its anterior sutural margin with the prefrontal; the left one is almost complete, preserved posteriorly up to the level of the subtemporal fenestra. The portion lateral to the orbit is only 5 mm in depth, the orbits being close to the lateral margin of the skull and the skull roof being rather flat.

In combining information from both orbits, orbital shape can be reconstructed and the length of the orbital diameters estimated. The right orbit lacks the posterior portion but preserves the anterior margin and most of the lateral and medial ones (mediolateral diameter equals 25 mm). The left orbit is less complete but the orbital contribution of left jugal is entirely preserved, allowing to estimate where the lateral margin turned upwards to form the posterior margin and, consequently, the length of the longer axis (about 40 mm long). The reconstructed orbits, facing dorsolaterally, are oval in shape, with the longer axis parallel to the lateral margins of the skull, and are located at the level of the anterior half of the interpterygoid vacuities. The orbits appear also relatively large in size with a comparatively low interorbital distance: the distance between the medial margin of the orbit and the median sagittal plane of the skull is less than the maximum mediolateral diameter of the orbit. The orbits of MSNM V2993 are larger and closer to the midline than those of *Trematosaurus madagascariensis* (Lehman, 1979) and *Tertrema acuta* (Wiman, 1917), and even more than those of *Trematosaurus brauni* (Schoch & Milner, 2000); in both size and distance, they match those of *Tertremoides ambilobensis* (Lehman, 1979) and of the large, adult specimen of *Trematolestes hagdorni* (Schoch, 2006); they are smaller and more separated from each other than those of the juvenile specimen of *Trematolestes hagdorni* (Schoch, 2006). Some indeterminate, displaced, poorly preserved, and large bones are visible within the left orbital cavity.

Palate (Fig. 4 A) - Although incomplete, the palate of MSNM V2993 is preserved better than the skull roof, rendering it possible recognition of many anatomical features and detailed comparisons with known trematosaurid palates. The preserved lateral margins of the skull of MSNM V2993 are straight in outline, without the change in curvature at the level of the choane (reducing the degree of convergence of the two maxillae before their contacts with the premaxillae) visible in *Tertrema acuta* (Wiman, 1917), *Hyperokinodon keuperinus* (Hellrung, 1987), and *Trematolestes hagdorni* (Schoch, 2006).

The snout is incomplete, truncated anteriorly at the level of the posteromedial borders of the anterior palatal vacuities. As a consequence, the premaxillae are almost entirely missing, with the exception of few millimetres of their ventral surfaces, preserved on both sides, just anterior to the suture with the maxilla. The choanae are sub-oval and elongate, although not so much elongated as in *Tertrema acuta* (Wiman, 1917), and do not appear particularly large. In size and shape they resemble those of *Trematosaurus brauni* (Schoch & Milner, 2000). Each choana is bordered by the vomer anteromedially, by the maxilla laterally, and by the palatine posteriorly. The vomers are almost complete, with a vomerine plate considerably longer than wide. Anteriorly, they form the posterior, rounded borders of the anterior palatal vacuities and, via a narrow process, the preserved medial borders too. In MSNM V2993, this narrow anterior process of the vomers is only slightly wider than the posterior margin of each anterior palatal vacuity. It is similarly narrow in the Malagasy snout referred to *Tertrema* by Lehman (1979), whereas it is markedly wider in *Trematosaurus brauni* (Schoch & Milner, 2000), *Tertrema acuta* (Wiman, 1917), *Hyperokinodon keuperinus* (Hellrung, 1987), and *Trematolestes hagdorni* (Schoch, 2006), in which it results about as wide as the two vacuities.

Anterior to the choanae, each vomer extends laterally up to the maxillary tooth row and bears a couple of very large, rounded, anteroposteriorly aligned sockets for the vomerine tusks; only the right anterior and the left posterior sockets are actually occupied by vomerine tusks (preserved as asymmetrical holes in Fig. 1). These big tusks, up to 16 mm tall, are conical and finely striated apicobasally. A pair of vomerine teeth as large as the maxillary ones is also present, located parallel to the choana and more clearly visible on the left side. A row of vomerine teeth parallel to the choana has been figured also in *Trematosaurus brauni* (Schoch & Milner, 2000: fig. 77). Large vomerine tusks are present also in *Trematolestes* (Schoch, 2006), *Tertrema* (Wiman, 1917), *Hyperokinodon keuperinus* (Hellrung, 1987), and *Trematosaurus brauni* (Schoch & Milner, 2000), although in the latter they are not as wide as in the other three taxa mentioned and in MSNM V2993. The denticulated suture between the vomers and the palatines can be traced with continuity only at the anterior and posterior extremities, close to the choanae and the interpterygoid vacuities respectively. The vomers extend posteriorly forming a sub-rectangular process that borders the anterior trait of the medial side of the interpterygoid vacuities. This process, apparently comparable in length with one figured by Wiman (1917) in *Tertrema acuta* and shorter than those of the other trematosaurids such as *Trematosaurus brauni* (Schoch & Milner, 2000), underplates the anterior portion of the cultriform process of the parasphenoid.

The cultriform process of the parasphenoid of MSNM V2993 has parallel lateral margins and is posteriorly preserved up to the level of the suture between the anterior branch of the pterygoid and the ectopterygoid. Interestingly, the cultriform process of MSNM V2993 shows features uncommon in the other trematosaurids: the preserved

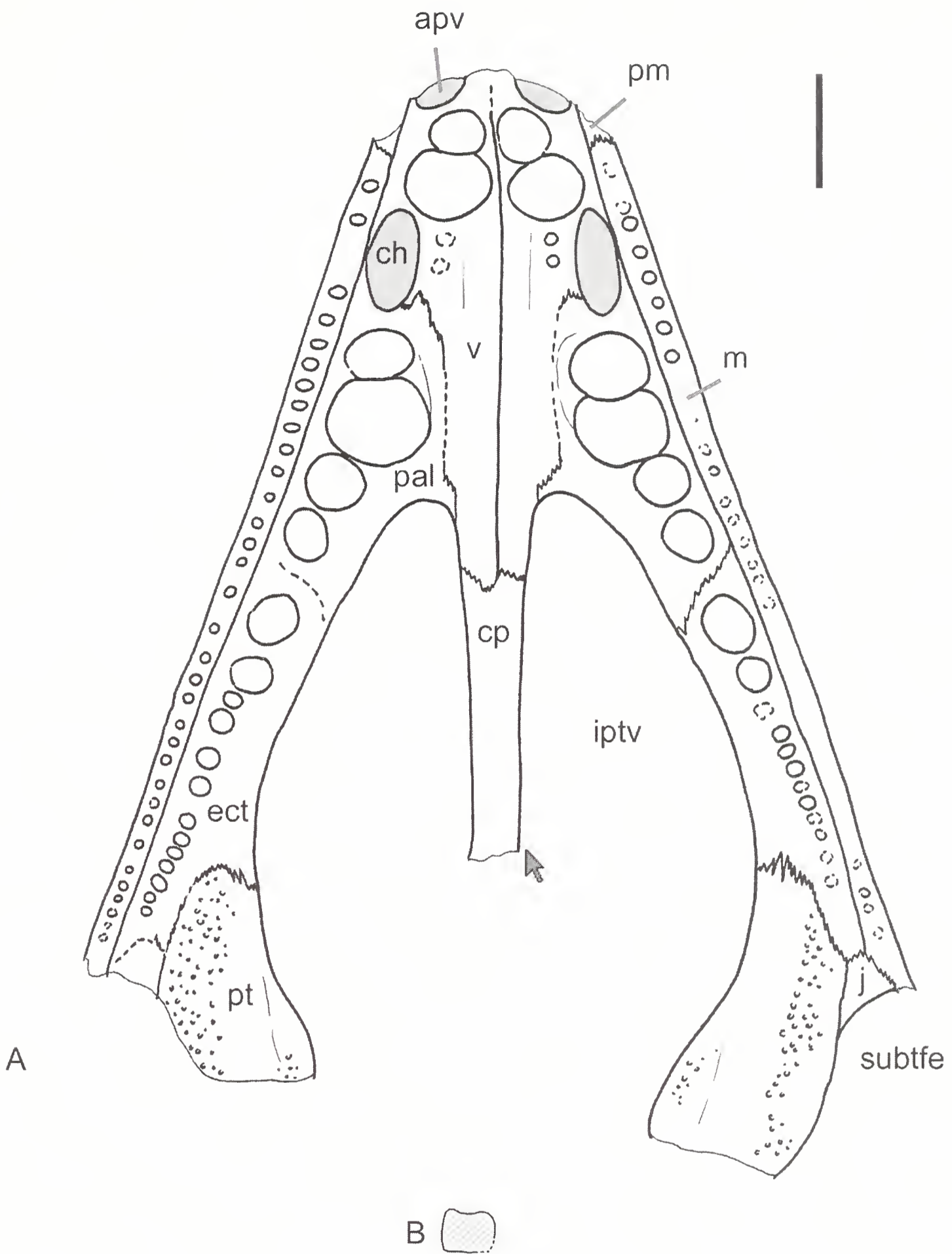


Fig. 4 - Interpretative line-drawing of the specimen MSNM V2993 in palatal view (A), and cross section of the cultriform process of the parasphenoid (B). The grey arrow in (A) indicates at which level of the cultriform process the cross section in (B) was drawn. Anatomical abbreviations: apv) anterior palatal vacuity; ch) choana; cp) cultriform process of the parasphenoid; ect) ectopterygoid; iptv) interpterygoid vacuity; j) jugal; m) maxilla; pal) palatine; pm) premaxilla; pt) pterygoid; subtfe) subtemporal fenestra; v) vomer. Scale bar equals 20 mm. (Drawings by SM).

Fig. 4 - Disegno dell'esemplare MSNM V2993 in norma palatale (A) e sezione trasversa del processo cultriforme del parasfenoide (B). La freccia grigia in (A) indica a che altezza del processo cultriforme è stata disegnata la sezione trasversa in (B). Abbreviazioni anatomiche: apv) vacuità palatale anteriore; ch) coana; cp) processo cultriforme del parasfenoide; ect) ectopterigoide; iptv) vacuità interpterigoidea; j) giugale; m) mascellare; pal) palatino; pm) premascellare; pt) pterigoide; subtfe) finestra subtemporale; v) vomere. La scala metrica equivale a 20 mm. (Disegni di SM).

portion is flat ventrally and squared in cross section (as suggested by Warren, 1998, for *Tertremoides ambilobensis*), as shown by the cross-sectional view of the broken posterior margin (Fig. 4 B), without any trace of the ventral keel recognized as a trematosaurid synapomorphy in recent phylogenetic reviews of the group (e.g., Steyer, 2002; Damiani & Yates, 2003; Schoch, 2006); the process is relatively wide, about twice the width of the mediolateral diameter of the dentigerous surface of the maxilla, whereas it is as wide as this surface in *Trematosaurus brauni* (Schoch & Milner, 2000), *Tertrema acuta* (Wiman, 1917), and *Trematolestes hagdorni* (Schoch, 2006).

Both palatines are well preserved and are similar in shape to those of *Trematosaurus brauni* (Schoch & Milner, 2000), the main difference consisting of size and number of palatine tusks and teeth: in MSNM V2993 the palatine dentition indeed consists of a row of four anteroposteriorly aligned large sockets bearing tusks (the first and the fourth sockets are still occupied by tusks on the right palatine, the first and the third on the left one), the first two extremely large (with tusks up to 16 mm in reconstructed height) and similar in size and shape to those borne by the vomers; in *Trematosaurus brauni* each palatine tooth row is composed by a total of six sockets, the first two hosting large tusks, the following four hosting teeth as large as or slightly larger than the maxillary teeth (Schoch & Milner, 2000: fig. 77). There are seven sockets in *Trematolestes hagdorni*, in which there is an additional tooth (Schoch, 2006: fig. 4 B). Four, possibly five, sockets, with two large tusks followed by two small tusks and a tooth as large as the maxillary ones lateral to the choana, seem to be present in *Tertrema acuta* but bone sutures are difficult to be seen in the image published by Wiman (1917: pl. XII).

In MSNM V2993, the denticulated suture between the palatine and ectopterygoid, well visible on the left side, is posteromedially directed at an angle of 60° respect to the tooth row and measures 20 mm in length. The right and left ectopterygoid are also entirely preserved, each one bearing a tooth row that is parallel to the maxillary tooth row and is in continuity with the palatine ones. The ectopterygoid tooth row consists of two tusks slightly smaller than the preceding palatine ones followed by several teeth, at least 14 on the right side, sub-circular in cross section and decreasing in size (from 4 to 2 mm in socket diameter) towards the posterior end of the row, where they match the size of the maxillary teeth. In *Trematosaurus brauni* the ectopterygoid does not bear tusks and the teeth are more than 20 in number (Schoch & Milner, 2000). A pair of tusks followed by 15 teeth are present in *Trematolestes hagdorni* (Schoch, 2006). At least one large tusk and more than 10 large teeth are present in *Tertrema acuta* (Wiman, 1917).

Aside from the tooth size and number, another difference regards the relative length of the ectopterygoid. In MSNM V2993 the ectopterygoid is as long as the vomerine plate (about 70 mm), as is the case in *Trematolestes hagdorni* (Schoch, 2006) and probably in *Tertrema acuta* (Wiman, 1917); it appears relatively shorter than that of *Trematosaurus brauni*, where it is almost twice the length of the vomerine plate (Schoch & Milner, 2000: fig. 77). The different relative length of the palate between MSNM V2993 and *Trematosaurus brauni* is suggested also by the interpterygoid vacuities, that, although similar in the general shape ("D" - shaped; see Fig. 4 and Schoch & Milner, 2000: fig. 77), appear considerably more stretched anteroposteriorly in the latter.

Of both pterygoids, only part of the anterior branch is preserved, and it has a granular ventral surface. The anterior branches seem to inflate mediolaterally towards their posteriormost preserved portion, forming a slightly convex medial

margin, and interrupting the regular, concave curvature of the lateral surface of the interpterygoid vacuities. This pattern is visible also in dorsal view.

A small portion of the left jugal appears as a wedge between the anterior branch of the pterygoid, the ectopterygoid, and the maxilla. As in *Trematosaurus brauni*, it borders the anterior margin of the subtemporal fenestra. The posteriormost tips of the maxillae bordering the anterolateral corner of the subtemporal fenestrae are missing, but, in all likelihood, the entire maxillary tooth row is preserved, more clearly visible on the right element. Unfortunately, only the empty sockets of the maxillary teeth are preserved: they are sub-circular in cross section, only slightly more compressed anteroposteriorly lateral to the palatines. Their diameters range from 2 to 2.5 mm. Numerous and delicate maxillary teeth are indicated by Schoch (2006) as a derived character shared by *Trematolestes hagdorni*, *Tertremoides madagascariensis*, and the lonchorhynchine trematosaurids. In MSNM V2993, the separation between the maxilla and the palatal elements medial to it is marked by a shallow longitudinal groove. This groove separates the maxillary tooth row from the palatal tooth row, possibly accommodating the tip of the teeth of the dentary tooth row, when the jaws closed (see Palaeobiology).

Discussion

Taxonomic affinities - MSNM V2993 certainly does not belong to *Wantzosaurus elongatus*, the latter having: more elongate interpterygoid vacuities with orbits more posteriorly retracted respect to them and considerably longer frontals and nasals already in juveniles; palatine that seems to be excluded from the interpterygoid vacuity by contact between a posterior process of the vomer and the ectopterygoid; palatine bearing two tusks only; vomerine plate bearing only one tusk and no tooth or denticle medial to each choana; a cultriform process of the parasphenoid that is definitely knife-edged.

In spite of the limited amount of possible direct comparisons within MSNM V2993 and the other trematosaurian specimens from Madagascar, the comparable anatomical features are consistent with the assignment of MSNM V2993 to *Tertremoides madagascariensis*, the only other Malagasy species we regarded as valid. As a matter of fact, size, shape, position, and orientation of the orbits, the inferred distance between orbits and nares, and skull outline and proportions in MSNM V2993 well match the scheme shown by other specimens of *Tertremoides madagascariensis*. The same combination of features renders weaker a possible attribution of MSNM V2993 to either *Tertrema*, or *Trematolestes*, or *Trematosaurus*, or the poorly known *Hyperokynodon*. Only the anterior extension of the frontals seems to be less in MSNM V2993 than in known specimens of *Tertremoides madagascariensis* but it must be taken into account that the nasofrontal suture has been only tentatively identified in the former, and clearly reported in only one specimen of the latter (Lehman, 1979: fig. 3).

Further comparisons between MSNM V2993 and other trematosaurids are made looking at the palate, although some palatal features of *Tertrema acuta* are poorly known and most of the palatal anatomy of *Trematolestes hagdorni* is from juvenile individuals (Schoch, 2006): MSNM V2993 resembles *Trematosaurus brauni* in size and shape of the choanae and in having a tooth row parallel to the choana - a plesiomorphic character according to Schoch (2006); MSNM V2993 resembles both *Tertrema acuta* and *Trematolestes hagdorni* in the ectopterygoid proportions

and in having very large vomerine tusks; MSNM V2993 resembles *Tertrema acuta* in having a short posterior process of the vomers underplating the cultriform process of the parasphenoid, and in having 4 palatine tusks (followed by a tooth in the latter); MSNM V2993 resembles *Trematolestes hagdorni*, *Tertremoides madagascariensis*, and the lonchorhynchine trematosaurids in having small, numerous, delicate maxillary teeth; finally, MSNM V2993 resembles *Trematolestes hagdorni* in size and number of ectopterygoid tusks and teeth.

The specimen MSNM V2993 differs from *Tertrema acuta*, *Trematolestes hagdorni*, and *Trematosaurus brauni* in having a considerably narrower anterior process of the vomers, and a wider cultriform process with a flat ventral surface and without any trace of ventral keel. As mentioned above, a knife-edged and narrow cultriform process has been recognized as a trematosaurid synapomorphy in recent phylogenetic reviews of the group (e.g., Steyer, 2002; Damiani & Yates, 2003; Schoch, 2006). Therefore, the plesiomorphic state shown by MSNM V2993 may eventually represent either a plesiomorphic trait, or an autapomorphic reversion occurred only in this Malagasy taxon (see description).

In conclusion, MSNM V2993 shows more affinities with *Tertrema acuta* and *Trematolestes hagdorni* than *Trematosaurus brauni* (albeit some affinities are found with the latter), and some peculiar features unreported in trematosaurids. This combination of features demonstrates the presence of - at least - one Malagasy trematosaurid genus clearly distinct from the long-snouted *Wantzosaurus* in the fauna, and not referable either to *Trematosaurus* or to other genera known outside Madagascar.

In our opinion, the Malagasy snout assigned by Lehman (1979: figs. 1, 2; pl. I A, B) to *Tertrema* should not be referred to this genus. Like the holotype of *Tertrema*, that Malagasy specimen has indeed a truncated tip of the snout, very large and elongate anterior palatal vacuities, and a depression on the posterior median process of the premaxillae (Lehman, 1979); however, it differs from *Tertrema* (Wiman, 1917) in having more rounded lateral margins of the snout, considerably less elongate nares, and, above all, for its peculiar, large premaxillary teeth, one of which located above the interpremaxillary suture. This peculiar tooth arrangement is not present in the other trematosaurid taxa considered in this study, although two large teeth are present in the tip of the snout of *Trematolestes* and teeth becoming progressively larger towards the anterior portion of the snout were described and figured by Lehman (1966: pl. VI A, B) for *Tertremoides madagascariensis*. A truncated tip of the snout is present, for example, also in *Trematosaurus brauni*, and large vomerine sockets are present in *Trematosaurus brauni*, *Tertrema acuta*, *Trematolestes hagdorni*, and MSNM V2993. Therefore, in our opinion Lehman's Malagasy snout should be assigned neither to *Tertrema* nor to *Trematosaurus* nor to *Trematolestes*. Rather, the few comparable features between Lehman's specimen and MSNM V2993 (e.g., narrow anterior median vomerine process, size and number of tusks) suggest that they may belong to the same taxon.

The only other, possibly non-lonchorhynchine trematosaurid palate from Madagascar is the specimen figured by Lehman (1961: pl. III E) and referred to an indeterminate trematosaurian. Comparisons between this specimen and MSNM V2993 cannot be made, because the former consists of more posterior elements (incomplete pterygoids and a parasphenoid plate with the posterior portion of the cultriform process) and, moreover, it is preserved in dorsal view.

Phylogenetic affinities - A phylogenetic analysis of stereospondylomorphs, based on 45 taxa and 86 cranial and mandibular characters, was conducted by Maganuco *et al.* (in press). That analysis was focussed on the affinities of the capitosaur *Edingerella madagascariensis* but included the main lineages of stereospondyls. From that study, we borrow the character descriptions and the data matrix. The present study is focussed on the phylogenetic position of both MSNM V2993 and non-Lonchorhynchinae Malagasy trematosaurids within the Trematosauria. For this reason, we add the following 9 operative taxonomic units (source see Appendix 1; codings see Appendix 2) for a total of 54 terminal taxa: the new specimen MSNM V2993; the Malagasy trematosaurid snout described by Lehman (1979) and referred by him to the genus *Tertrema*; the Malagasy species *Trematosaurus madagascariensis* and *Tertremoides ambilobensis* (coded separately, to test their synonymy); and further five species of trematosaurids, *Aphaneramma rostratum*, *Cosgriffius campi*, *Lyrocephaliscus euri*, *Platystega depressa*, and *Tertrema acuta*. The final data matrix, compiled in NDE (Page, 2001), was analyzed using the heuristic search of the most parsimonious tree (MPT) of PAUP 4.0b10 (Swofford, 2002). Character transformation was optimized under both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options of PAUP. The analysis generated 420 most parsimonious trees (MPTs), requiring 517 steps, and giving a consistency index (CI) of 0.2263, a retention index (RI) of 0.6444, and a rescaled consistency index (RC) of 0.1458. The majority-rule consensus tree of the 420 MPTs is illustrated in Fig. 5. The discussion below is based on this consensus tree, and the 'tree description' option of PAUP was used to obtain the reconstructed states for internal nodes (Tab. 1), based on one of the MPTs showing a topology identical to that of the majority-rule consensus tree. A detailed investigation of the non-trematosaurian stereospondyl interrelationships is beyond the scope of this study. Relationships between the non-trematosaurian taxa are discussed in Maganuco *et al.* (in press) and will be discussed in more details elsewhere (Maganuco *et al.*, in prep.). We note, however, that the addition of several trematosaurid terminal taxa did not affect the global tree topology obtained by Maganuco *et al.* (in press), the main difference consisting of the position of *Lapillopsis*, *Lydekkerina*, *Chomatobatrachus*, and *Deltacephalus*: in the present analysis, these taxa are found to be basal to the short-faced stereospondyl clade and not strictly related to the Capitosauria + Trematosauria; on the contrary, in Maganuco *et al.* (in press) *Lapillopsis* is a basal stereospondyl, whereas the other three taxa are successive sister taxa of the Capitosauria + Trematosauria and not strictly related to the short-faced stereospondyl clade.

As regards trematosaurids, the present analysis suggests that MSNM V2993, the Malagasy snout referred to *Tertrema* by Lehman (1979), and the remains assigned so far to *Tertremoides ambilobensis* or *Trematosaurus madagascariensis* may well have pertained to a single species, *Tertremoides madagascariensis sensu* Schoch & Milner (2000), pending a detailed revision of Lehman's material housed at the Muséum national d'Histoire naturelle, Paris, France. The group consisting of this possibly monospecific Malagasy non-Lonchorhynchinae material is closely related to the German species *Trematolestes hagdorni*, forming the '*Trematolestes* clade' of Schoch (2006). It is noteworthy that in some of the MPTs, *Trematolestes hagdorni* results alternatively the sister taxon of one of the Malagasy specimens/species: this is probably linked to the fact that the Malagasy specimens/species are poorly known in many characters. Therefore, relationships within the '*Trematolestes* clade'

can not be well elucidated, based on the phylogeny only. The topology in Fig. 5, showing *Trematolestes hagdorni* as sister taxon of a monophyletic Malagasy material, is, however, the most likely, taking into account also the taxonomic affinities discussed above and the geological/stratigraphical context. As in Schoch (2006), the ‘*Trematolestes* clade’ is nested within the slender-headed trematosaurids but, contrary to that author, among these it is more closely related to *Tertrema acuta* than to the lonchorhynchine trematosaurids. The Lonchorhynchinae as represented here form a monophylum with *Aphaneramma rostratum* as the basalmost member. The internal relationships differ from those found by Schoch (2006), in which *Wantzosaurus elongatus* is the basalmost of the three taxa. However, as noted by Schoch (2006), relationships within the Lonchorhynchinae can be affected by the fact that *Aphaneramma rostratum* is poorly known in many characters. *Lyrocephaliscus euri*, *Trematosaurus brauni*, and *Platystega depressa* are stem-taxa of the recognized monophylum of slender-headed trematosaurids, forming an unresolved polytomy in the strict consensus tree. According to the majority-rule consensus tree in Fig. 5, the former species would be the most basal of the three species, whereas the latter one would be the most derived. *Angusaurus* and *Thoosuchus yakovlevi* are found to be basal Trematosauroida (*sensu* Yates & Warren 2000, i.e., the last common ancestor of *Thoosuchus* and *Trematosaurus brauni* and all its descendants), with the latter being the most basal of the two. We follow Yates & Warren (2000) redefining the Trematosauria Romer, 1947 as all stereospondyls sharing a more recent common ancestor with *Trematosaurus* than with *Parotosuchus*. Our Trematosauria is therefore formed by *Benthosuchus sushkini* plus the Trematosauroida, and results the sister taxon of the Capitosauria (we follow Damiani & Yates, 2003 redefining the Capitosauria Yates & Warren, 2000 as all stereospondyls sharing a more recent common ancestor with *Parotosuchus* than with *Trematosaurus*).

Systematic assignment - As mentioned, in Schoch’s (2006) phylogeny *Trematolestes hagdorni* is the sister taxon of *Tertremoides madagascariensis*: they plus the Lonchorhynchinae form the sister taxon of *Tertrema acuta*, whereas *Trematosaurus brauni* is a basal trematosaurid not strictly linked with the Malagasy taxon, as formerly recognized by Schoch & Milner (2000). The phylogenetic affinities within *Tertremoides madagascariensis* and the other trematosaurids as found by Schoch

Fig. 5 - Majority-Rule consensus tree of 420 MPTs resulting from a phylogenetic analysis using software PAUP* Version 4.0b10 (Swofford, 2002) based on the data matrix of Maganuco *et al.* (in press), with nine new OTUs added (sources see Appendix 1; codings see Appendix 2). TL=517 steps, CI=0.2263, RI=0.6444, RC=0.1458. Percentages at nodes are indicated only for groups appearing on less than 100% of the MPTs. Abbreviations: A) Stereospondyli; B) short-faced stereospondyl clade; C) Capitosauria; D) Trematosauria; E) Trematosauroida; F) slender-headed trematosaurids; G) Lonchorhynchinae; H) ‘*Trematolestes* clade’, *sensu* Schoch, 2006; I) *Tertremoides madagascariensis*, *sensu* Schoch & Milner, 2000.

Fig. 5 - Albero “Majority-Rule consensus” dei 420 alberi più parsimoniosi (MPTs) generati da PAUP* 4.0.b10 (Swofford, 2002) sulla base della matrice dei dati riportata da Maganuco *et al.* (in press), in cui sono state aggiunte nove nuove unità operative tassonomiche (OTUs) (fonti in Appendice 1; codifiche in Appendice 2). TL=517 steps, CI=0.2263, RI=0.6444, RC=0.1458. Le percentuali ai nodi sono indicate solo per quei gruppi che non appaiono nel 100% dei MPTs. Abbreviazioni: A) Stereospondyli; B) clade degli stereospondili a muso corto; C) Capitosauria; D) Trematosauria; E) Trematosauroida; F) clade dei trematosauri dal muso slanciato; G) Lonchorhynchinae; H) ‘clade di *Trematolestes*’, *sensu* Schoch, 2006; I) *Tertremoides madagascariensis*, *sensu* Schoch & Milner, 2000.



Tab. 1 - Unambiguous apomorphies, additional apomorphies under delayed character-state optimization (DELTRAN), and additional apomorphies under accelerated character-state optimization (ACCTRAN), describing trematosaurian nodes and terminal taxa in Fig. 5. The clade notation used in the Node column, "taxon X + taxon Y", refers to the least inclusive clade in the Majority-Rule consensus tree comprising the two given taxa, and does not imply that these taxa share a direct sister-taxon relationship. Abbreviations, systematic terms, and informal names used in Fig. 5 to define some clades are also indicated in the Node column. The symbol "→" indicates the character-state change occurred.

Tab. 1 - Apomorfie non ambigue, apomorfie addizionali ottenute tramite l'ottimizzazione ritardata dello stato dei caratteri (DELTRAN) e apomorfie addizionali ottenute tramite l'ottimizzazione accelerata dello stato dei caratteri (ACCTRAN) che descrivono i nodi e i taxa terminali di trematosauri visibili in Fig. 5. I cladi sono indicati nella colonna dei nodi tramite la dicitura "taxon X + taxon Y": essa si riferisce al clade meno inclusivo dell'albero di consenso Majority-Rule che comprende i due taxa dati e non implica una diretta relazione di tipo "sister-taxon" tra di essi. Nella colonna dei nodi sono indicati anche le abbreviazioni, i termini sistematici e i nomi informali utilizzati in Fig. 5 per definire alcuni cladi. Il simbolo "→" indica il cambiamento di stato avvenuto ad ogni nodo per ciascun carattere.

Node / terminal taxon	Unambiguous apomorphies	Additional apomorphies (DELTRAN)	Additional apomorphies (ACCTRAN)
Trematosauria + Capitosauria	77 (0→1); 78 (0→1); 81 (0→1).	8 (0→1).	28 (0→1).
D , Trematosauria	3 (0→1); 4 (0→1); 6 (0→1); 9 (0→1); 21 (0→1); 23 (0→1); 24 (0→1); 25 (0→1); 26 (0→1); 45 (0→1); 50 (1→2); 55 (0→2); 68 (0→1).	57 (0→1).	None.
<i>Benthosuchus sushkini</i>	5 (0→2); 7 (0→1); 12 (0→1); 46 (0→1); 47 (0→1); 57 (1→2); 80 (0→1).	28 (0→1); 39 (0→1); 54 (2→0).	None.
E , Trematosauroida	11 (0→1); 20 (0→1); 52 (1→2); 58 (1→2); 59 (1→0); 67 (0→1); 69 (0→1); 83 (0→1); 84 (0→1); 85 (0→1); 86 (0→1).	None.	28 (1→0); 34 (1→0); 39 (1→0); 54 (0→2).
<i>Thoosuchus yakovlevi</i>	29 (0→1); 38 (0→2); 72 (0→1).	34 (1→0).	None.
<i>Angusaurus</i> + <i>Wantzosaurus elongatus</i>	31 (0→1); 65 (0→1).	34 (1→3);	34 (0→3).
<i>Angusaurus</i>	47 (0→1).	None.	None.
<i>Lyrocephaliscus euri</i> + <i>Wantzosaurus elongatus</i>	5 (0→1); 13 (0→1); 40 (0→1); 49 (0→1); 71 (0→2).	None.	9 (1→0).
<i>Lyrocephaliscus euri</i>	2 (1→0); 4 (1→0); 6 (1→0); 19 (0→1); 24 (1→0); 55 (2→1); 64 (0→1).	9 (1→0); 34 (3→0).	34 (3→0).

<i>Trematosaurus brauni</i> + <i>Wantzosaurus elongatus</i>	53 (0→1); 70 (0→1).	None.	38 (0→2).
<i>Trematosaurus brauni</i>	54 (2→1); 59 (0→1).	38 (0→2).	9 (0→1).
<i>Platystega depressa</i> + <i>Wantzosaurus elongatus</i>	18 (0→1).	None.	77 (1→0).
<i>Platystega depressa</i>	5 (1→0); 8 (1→0); 19 (0→2); 68 (1→0).	34 (3→0).	34 (3→0).
F , slender-headed trematosaurs (<i>Trematolestes hagdorni</i> + <i>Wantzosaurus elongatus</i>)	47 (0→1).	77 (1→0).	33 (1→0).
G , Lonchorhynchinae	4 (1→2); 5 (1→2); 14 (0→1); 58 (2→1).	None.	84 (1→0).
<i>Aphaneramma rostratum</i>	24 (1→0); 31 (1→0); 37 (1→2).	84 (1→0);	33 (0→1); 38 (2→0); 57 (0→1).
<i>Cosgriffus campi</i> + <i>Wantzosaurus elongatus</i>	13 (1→0); 15 (0→1); 59 (0→1).	57 (1→0).	54 (2→0); 70 (1→0).
<i>Cosgriffus campi</i>	6 (1→0); 52 (2→0).	None.	None.
<i>Wantzosaurus elongatus</i>	26 (1→0); 34 (3→1); 51 (0→2); 68 (1→0).	33 (1→0); 38 (0→2); 54 (2→0); 70 (1→0).	None.
<i>Trematolestes hagdorni</i> + <i>Tertrema acuta</i>	51 (0→1); 64 (0→2).	9 (1→0); 33 (1→0).	40 (1→0); 81 (1→0).
<i>Tertrema acuta</i>	31 (1→0); 37 (1→0); 47 (1→2); 68 (1→0).	38 (0→2); 51 (1→2).	None.
H , ‘ <i>Trematolestes</i> clade’ (<i>Trematolestes hagdorni</i> + MSNM V2993)	8 (1→0); 10 (0→2); 13 (1→0); 16 (0→1); 26 (1→0).	57 (1→0).	38 (2→0); 73 (0→1).
<i>Trematolestes hagdorni</i>	4 (1→0).	51 (1→2); 73 (0→1); 81 (1→0).	None.
I , <i>Tertremoides madagascariensis</i> (<i>Trematosaurus madagascariensis</i> + MSNM V2993)	None.	40 (1→0).	19 (0→1); 44 (0→1); 51 (2→1); 53 (1→0); 54 (2→1); 67 (1→0); 69 (1→2).
<i>Trematosaurus madagascariensis</i>	None.	19 (0→1); 44 (0→1).	None.
MSNM V2993 + Malagasy “ <i>Tertrema</i> ” snout	None.	53 (1→0).	None.
Malagasy “ <i>Tertrema</i> ” snout	None.	54 (2→1).	None.
MSNM V2993	None.	67 (1→0); 69 (1→2).	None.

(2006) are consistent with the phylogenetic affinities found in this study and with taxonomic affinities found between MSNM V2993 and the other trematosaurids based on palatal features (as mentioned in the taxonomic affinities section above, MSNM V2993 shows more affinities with *Tertrema acuta* and *Trematolestes hagdorni* than *Trematosaurus brauni*, and has some peculiar features indicating that it belongs to another taxon). This is consistent also with the tentative attribution of MSNM V2993 to cf. *Tertremoides madagascariensis* we proposed above based on skull roof features and skull outline.

Therefore, we cautiously prefer to do not erect a new taxon for MSNM V2993, and - as already mentioned - we provisionally refer it, the snout described by Lehman (1979: figs. 1, 2; pl. IA, B) and the other Malagasy specimens - except from those belonging to *Wantosaurus elongatus* and the indeterminate trematosaurian palate figured by Lehman (1961, pl. III E) - to cf. *Tertremoides madagascariensis* (Lehman, 1966) Schoch & Milner, 2000, pending new, more complete material and a systematic revision of the material so far described. In the end, based on this systematic assignment, we also provide a tentative reconstruction of the palate of cf. *Tertremoides madagascariensis* (Fig. 6).

Size and ontogenetic stage - Interestingly, all the Malagasy specimens referable to *Tertremoides madagascariensis* are large individuals, up to 300 mm in estimated skull length (e.g., Fig. 6), and at the same time they are characterized by large orbits. Skull length is comparable to that of *Tertrema acuta* (Wiman, 1917), and surpasses by far that of adult individuals of *Trematosaurus brauni* (Schoch & Milner, 2000). The orbits of all the Malagasy specimens, MSNM V2993 included, are comparatively larger than those of *Tertrema acuta*, and even more than those of *Trematosaurus brauni*, whereas they are comparable in size to those of the adult skull of *Trematolestes hagdorni*; orbits as large as - or even larger - are retained also in adults of *Wantosaurus elongatus* (Steyer, 2002). Although absolute size taken alone is not a valid criterion to establish the growth stage (Steyer, 2000), those examples demonstrate that large orbits and adult size can coexist in some species of trematosaurids. Thus, MSNM V2993 and the other specimens of *Tertremoides madagascariensis* could represent either large juvenile individuals of very large trematosaurid species, or adult individuals characterized by retention of comparatively large orbits with reduced interorbital distance. Following Schoch (2006), we consider more plausible the second hypothesis.

Palaeobiology - The dentition of MSNM V2993 indicates a carnivorous diet. The small maxillary teeth and the enlarged palatal teeth formed two parallel rows, with the dentary tooth row fitting between the two upper ones, when the jaws closed. The pointed teeth, circular to oval in cross section, functioned as piercers and graspers rather than slashers and slicers or crushing surfaces. Trematosaurids are commonly regarded as piscivorous and aquatic, some of them clearly marine (e.g., Warren, 2000; Steyer, 2002). Assuming an aquatic mode of life for MSNM V2993, the dental apparatus, the interlocking jaw mechanism, the relatively narrow snout limiting drag in water, and the comparatively large body size would have made it one of the top predators of its ecosystem, well suitable to hold on rapid, slippery preys such as the coeval osteichthyan fishes (e.g., Beltan, 1996) and the soft-bodied invertebrates.

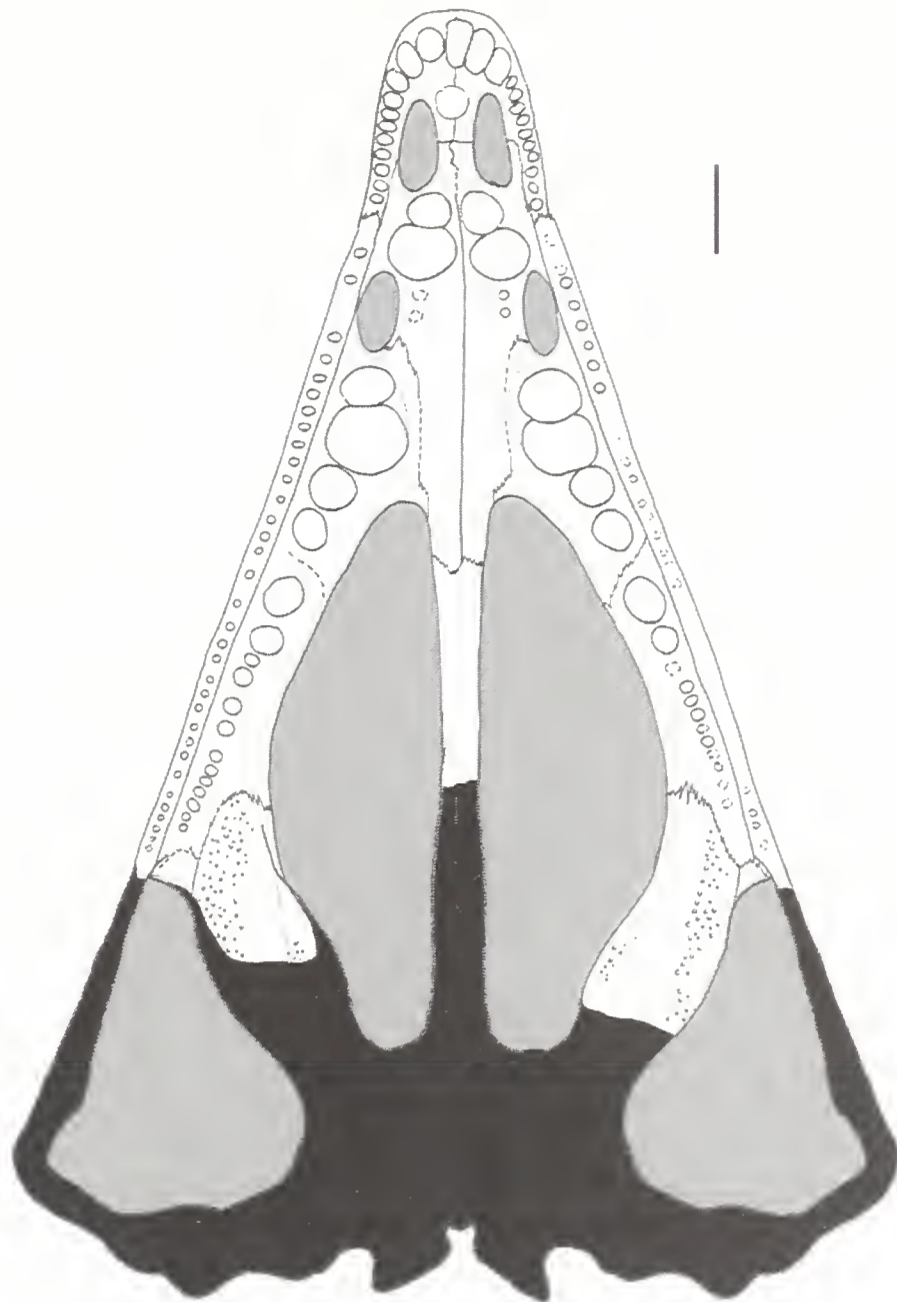


Fig. 6 - Tentative reconstruction of the skull of cf. *Tertremoides madagascariensis* in palatal view, starting from the specimen MSNM V2993. The tip of the snout is from the Malagasy specimen referred to 'Tertrema' by Lehman (1979). Unknown portions of the palate (in black) have been taken from *Trematolestes hagdorni* and adapted to the skull outline of cf. *Tertremoides madagascariensis*. Scale bar equals 20 mm. (Drawings by SM).

Fig. 6 - Ricostruzione tentativa del cranio di cf. *Tertremoides madagascariensis* in norma palatale, a partire dall'esemplare MSNM V2993. La porzione rostrale del muso è presa dall'esemplare malgascio riferito a 'Tertrema' da Lehman (1979). Le parti del palato sconosciute (in nero) sono state prese da *Trematolestes hagdorni* e adattate alla forma del cranio di cf. *Tertremoides madagascariensis*. La scala metrica equivale a 20 mm. (Disegni di SM).

Acknowledgements

We are grateful to the Ministère de l'Énergie et des Mines, and the Direction des Mines et de la Géologie de Madagascar (Antananarivo), for their indispensable collaboration. Many thanks also to the people of the villages in the neighbourhood of Anaborano Ifasy for their kind help in the field. The manuscript benefited greatly from reviews by J. Sébastien Steyer (MNHN) and Massimo Delfino (Università degli Studi di Firenze). We thank also Giorgio Teruzzi for access to specimens housed at MSNM, Daniel Goujet and Monette Vèran for access to specimens housed at MNHN, and Stefania Nosotti (MSNM) and Anna Marazzi for their useful advices about the presentation of the manuscript. Simone Maganuco thanks Stella Pomodoro for her preliminary work on the specimen, and Ilaria Vinassa Guaraldi de Regny (MSNM) and Cristiano Dal Sasso (MSNM) for their kind support. This research was supported by Vox Idee per il business S. r. l. (Milano, Italy).

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Ricevuto: 22 luglio 2008

Approvato: 6 agosto 2008

Appendix 1

Sources of data of the terminal taxa added in the present study.

<i>Aphaneramma rostratum</i>	Säve-Söderbergh (1935); Warren (2000).
<i>Cosgriffius campi</i>	Welles (1993).
<i>Lyrocephaliscus euri</i>	Säve-Söderbergh (1936); Schoch & Milner (2000).
<i>Platystega depressa</i>	Säve-Söderbergh (1936).
<i>Tertrema acuta</i>	Wiman (1917).
Malagasy “ <i>Tertrema</i> ” snout	Lehman (1979).
<i>Trematosaurus madagascariensis</i>	Lehman (1966, 1979); Janvier (1992).
<i>Tertremoides ambilobensis</i>	Lehman (1979).

